

**NEST BIOLOGY OF *OSMIA (DICERATOSMIA)*  
*SUBFASCIATA* CRESSON IN CENTRAL TEXAS  
(HYMENOPTERA: MEGACHILIDAE)**

JOHN L. NEFF<sup>1</sup> AND BERYL B. SIMPSON<sup>1,2</sup>

<sup>1</sup>Central Texas Melittological Institute, 7307 Running Rope,  
Austin, Texas 78731

<sup>2</sup>Department of Botany, The University of Texas, Austin, Texas 78713

*Abstract.*—Nests and provisioning behavior of *Osmia (Diceratosmia) subfasciata* Cresson, a widely distributed, polylectic, cavity nesting bee were studied in central Texas. Most study nests were in borings in pine blocks, but field observations suggest snail shells also are used. Nest plugs and partitions are formed of a mixture of masticated plant material and coarse sand with both materials collected and mixed on the same foraging trip. Provisioning series consist of a mix of long and short foraging trips, with six to ten long trips required to provision a cell. Details of the structure of the four layered cocoon are discussed and figured. Biologically novel features included the initiation of the outermost cocoon layer while the larva is still feeding with the margins of this layer being extended along the cell wall as feeding continues. Larvae spend part of the summer in an extended prepupal diapause before pupating and eclosing to overwinter within their natal cocoons. Floral pollen and nectar sources are listed and observations on the biology of *Chrysura pacifica* (Say) (Chrysididae), a nest parasite, are presented.

*Key Words.*—Insecta, bee, nest biology, provisioning rate, cocoon, diapause

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The subgenus *Diceratosmia* has been considered the most generalized group of North American *Osmia* (Sinha 1958). Although American workers long considered *Diceratosmia* to be a distinct genus, it was reduced to a subgenus of *Osmia* by Sinha (1958) in a treatment followed by most modern workers (Mitchell 1962, Hurd 1979, Michener 1979). *Osmia (Diceratosmia) subfasciata* Cresson is a widespread but little studied member of this assemblage with most observations on its biology consisting only of brief reports of its use of beetle burrows in wood as nest sites (Linsley 1946, Mitchell 1962), and collection records suggesting its use of mud wasp nests and plant stems as nest sites (Cockerell 1911). The only report yielding any details on its nesting biology is a brief note by Krombein (1967: 311–312) that described a single nest from Arizona, but gave little indication there is anything distinctive about the biology of this bee. Our observations agree in general outline with those of Krombein but differ significantly from his observations in several aspects of nest biology such as materials used in nest construction and duration of prepupal diapause. These differences, coupled with new data on provisioning behavior and timing of cocoon formation, suggest that *O. subfasciata* is biologically more interesting than previously indicated.

#### MATERIALS AND METHODS

Observations on foraging behavior and nest construction were conducted from 1979 to 1990 at several sites in central Texas with most of the studies done between 1986 and 1990 at the Brackenridge Field Laboratory (BFL) of the University of Texas, Austin, Texas. Artificial pine block trap-nests with diameters of 2.8, 3.2, 4.8 and 6.4 mm were set out at BFL as well as at Sayersville, Bastrop

Co., and Charco, Goliad Co. Additional nests with bores of 5.8, 7.9 and 9.5 mm were also set out at BFL. All 2.8 mm and some 3.2 mm diameter nests had bore depths of 45 mm. Most 3.2 mm nests and nests of all other diameters were bored to a depth of 120 mm. Nests were set out in both large, shaded domiciles with 40 to 60 nests per domicile or in smaller exposed clusters of 12 to 16 nests at BFL. Roughly equal numbers of nests of each diameter were used in each cluster or domicile. Nests in the large domiciles, but not in the small clusters, were replaced when empty nests were filled. The domiciles were placed 1 m from the ground on poles equipped with various sticky traps and moats to exclude fire ants. Nest clusters were taped or wired to tree limbs at 1 or 2 m above the ground as well as mounted on stakes at a height of 15 cm above the ground. Four sets of nest clusters were set out at Charco and Sayersville with two nest clusters on stakes and two on tree limbs at each site. All nests were aligned with their long axes horizontal to the ground.

Individual nests, or provisioning females, from BFL were coded by the year followed by the nest number. Data on phenology and floral hosts were based on the general collections and observations of JLN in central Texas from 1979 through 1989. Data are presented as the mean  $\pm$  one standard deviation. Plant nomenclature follows Correll & Johnston (1970) and Johnston (1988). Insect vouchers are deposited at the Brackenridge Field Laboratory, Austin, Texas and the Snow Museum, University of Kansas, Lawrence Kansas.

Observations on larval development were based on trap-nests opened in the laboratory and maintained at room temperature (24° C to 8° C summer and 15° C to 22° C winter). Torchio (1989) found that in several *Osmia* spp., the first larval molt occurs before hatching so that the first evident instar is actually the second yielding a total of five larval instars. Our methods were inadequate for detecting if such an early molt occurs in *O. subfasciata* so our discussion refers to the number of instars assuming the eclosing larva is the first instar although we recognize this may be incorrect.

Pollen collection records were based on field observations and analyses of samples of scopal loads and nest provisions. Pollen from scopal loads was mounted in glycerine for microscopic examination and sorted to plant morphospecies with the aid of a reference pollen collection. Crude pollen volume per morphospecies was estimated from pollen volume per grain times number of grains per sample (minimum of 200 grains for total sample). As a conservative measure, only pollens of species constituting 10% or more of the volume of a sample were considered to have been actively collected because some pollen will be picked up incidental to nectaring and many flowers may show high levels of "contamination" of foreign pollen which may be unintentionally collected by a bee.

## RESULTS

*Phenology and Floral Hosts.* — *Osmia subfasciata* is a strictly vernal species in central Texas. Collection records suggest the species is weakly protandrous with females having much greater longevity than males (Fig. 1). We have collected males from 3 Mar to 14 May in central Texas with most records from the last half of March, although females were collected from 14 Mar to 19 Jun with most activity from the last half of March through April. Lifespans of individual bees are unknown.



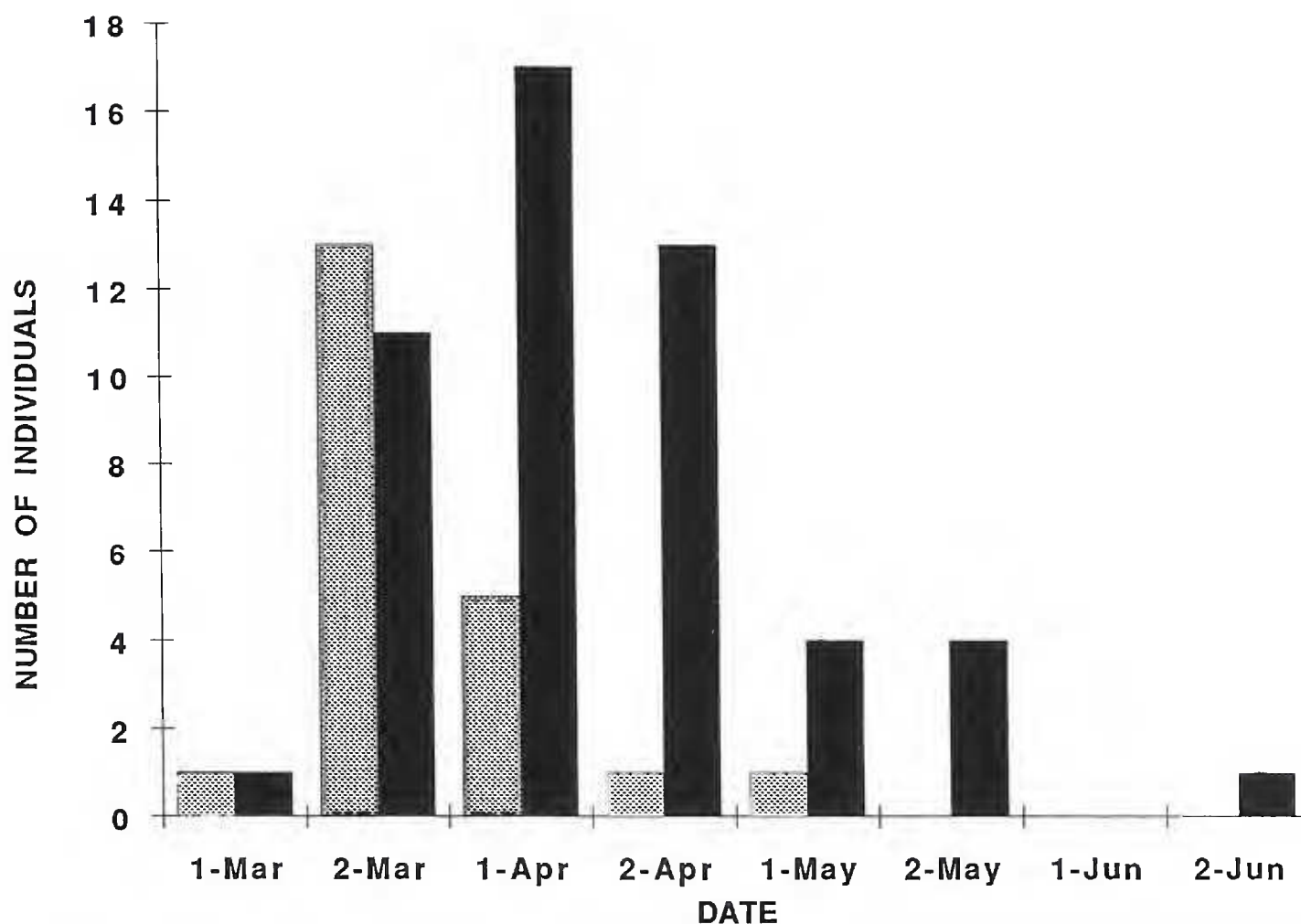


Figure 1. Central Texas collections records for *O. subfasciata* indicating pattern of seasonal abundance. Males = hatched bars. Females = solid bars. Horizontal axis in 2 week periods.

Females of *Osmia subfasciata* are clearly polylectic, collecting pollen from a wide array of plants. We recorded *O. subfasciata* visiting flowers of 32 genera in 14 families in central Texas (Table 1). Hurd & Michener (1955) listed an additional three families and nine genera of plants visited by *O. subfasciata* in Texas. Non-Texas records (Hurd & Michener 1955, Mitchell 1962) bring the total to 18 families and 48 genera. *Osmia subfasciata* collected pollen of at least 13 genera in nine families in central Texas (indicated by the letter P in Table 1). Analysis of pollen loads and nest contents from trap-nests indicated 54% (14 of 26) of the scopal loads contained mixtures of pollens (two or more pollens each representing at least 10% of pollen load volume).

**Nest Structure.**—Considerable variation in body size is seen in central Texas *O. subfasciata* with males usually smaller than females. Males were  $7.1 \pm 0.8$  mm (range 5.8–8.7;  $n = 25$ ) in length with thoracic widths of  $2.2 \pm 0.2$  mm (range, 1.8–2.6;  $n = 25$ ). Females were  $8.5 \pm 0.8$  mm (7.0–9.7;  $n = 25$ ) in length with thoracic widths averaging  $2.7 \pm 0.5$  mm (2.2–3.1;  $n = 25$ ). Females initiated nests in wooden traps with bore diameters of 3.2 ( $n = 4$ ), 4.8 ( $n = 11$ ) and 6.4 mm ( $n = 2$ ). Only the long 120 bores were used by *O. subfasciata*. Our sample of nests suggests diameters of 3.2 to 4.8 mm, a size best fitting observed female cross-sectional area, were the preferred nest diameters for *O. subfasciata*. Unlike many taxa collected during trap-nesting programs, *O. subfasciata* is apparently not gregarious as we never found more than one female active at a given trap-nest station.

As is common in *Osmia*, but not in some trap-nesting *Hoplitis*, nest walls were unlined, even in nests with diameters significantly larger than that of the cross-

Table 1. Central Texas floral records for *Osmia subfasciata*.

Plant family	Plant taxon	Visited by
Asteraceae	<i>Chaetopappa bellioides</i> (A. Gray) Shinnery	♂
	<i>Crepis</i> sp.	♀
	<i>Engelmannia pinnatifida</i> Nuttall	♂
	<i>Coreopsis nuecensis</i> Heller	♀
	<i>Coreopsis basalis</i> var. <i>wrightii</i> (A. Gray) Blake	♀
	<i>Erigeron</i> sp.	♀
	<i>Gaillardia pulchella</i> Fougereux	♀
	<i>Hymenoxys scaposa</i> (DC) Parker	♀P, ♂
	<i>Krigia occidentalis</i> Nuttall	♂
	<i>Lindheimera texana</i> Gray & Engelmann	♂
Berberidaceae	<i>Berberis swaseyi</i> Buckley	♂
Brassicaceae	<i>Lesquerella grandiflora</i> (Hooker) Watson	♀P
	<i>Lesquerella argyrea</i> (A. Gray) Watson	♀
Cactaceae	<i>Opuntia macrorhiza</i> Engelmann	♀
Commelinaceae	<i>Tinantia anomala</i> (Torrey) Clarke	♀P
Fabaceae	<i>Cercis canadensis</i> L.	♀, ♂
	<i>Desmanthus velutinus</i> Scheele	♀P
	<i>Lupinus texensis</i> Hooker	♀P
	<i>Prosopis glandulosa</i> Torrey	♀P, ♂
	<i>Vicia villosa</i> Roth	♂
	<i>Nama hispidum</i> A. Gray	♀P
Hydrophyllaceae	<i>Nemophila phacelioides</i> Nuttall	♀P, ♂
	<i>Phacelia congesta</i> Hooker	♀P
	<i>Phacelia patuliflora</i> (Engelmann & A. Gray) A. Gray	♀
	<i>Brazoria</i> sp.	♀
Lamiaceae	<i>Monarda citriodora</i> Cervantes	♀P
	<i>Teucrium cubense</i> Jacquin	♀, ♂
Malvaceae	<i>Callirhoe leiocarpa</i> Martin	♀
	<i>Callirhoe involucrata</i> (Torrey) A. Gray	♀P, ♂
	<i>Sida abutifolia</i> Miller	♀
	<i>Sphaeralcea lindheimeri</i> A. Gray	♀P
Onagraceae	<i>Oenothera speciosa</i> Nuttall	♀P
Rubiaceae	<i>Hedyotis nigricans</i> (Lamark) Fosbery	♀P
Sapindaceae	<i>Ungnadia speciosa</i> Endlicher	♂
Solanaceae	<i>Chamaesaracha sordida</i> (Dunal) A. Gray	♀
Verbenaceae	<i>Verbena bipinnatifida</i> Nuttall	♀
	<i>Verbena officinalis</i> L. ssp. <i>halei</i> (Small) Barber	♀, ♂

<sup>1</sup> P indicates known pollen host.

sectional diameter of the bee. Partitions, basal plugs and entrance plugs were constructed of a mixture of coarse sand and masticated plant material (Figs. 2, 3). The entrance plug was single layered, 3–6 mm thick, and had a smooth, concave outer surface. The margins of the plug were usually flush with, or more rarely recessed 3–6 mm from, the nest entrance. The entrance plug was followed by one or two vestibular cells of 6–47 mm in length. The partition between the vestibular cells, or the outermost cell partition, if only one vestibular cell was present, was consistently thicker than the inner brood cell partitions and sometimes thicker than the entrance plug. Partitions between inner cells were quite thin medially (0.2–0.3 mm) but thicker along the cell wall (0.5–1.0 mm). In one case, a female was found to have used a nest previously occupied by a eumenid wasp and had



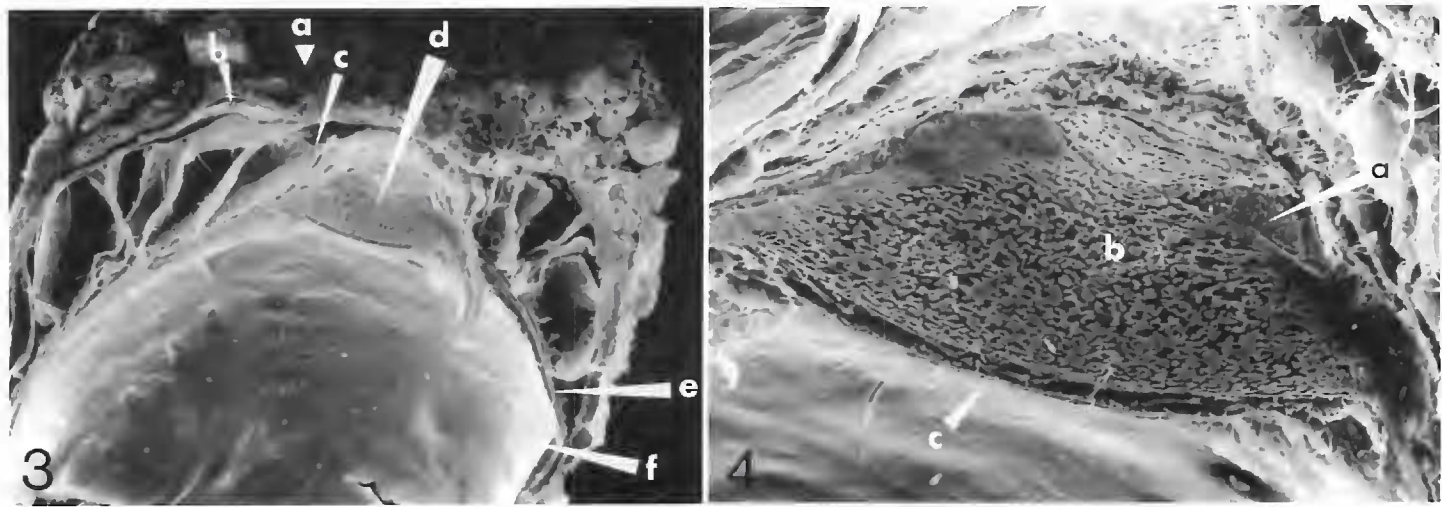
Figure 2. Female *O. subfasciata* adding soil to masticated leaf material (7 $\times$ ).

used portions of some of the remaining mud partitions as bases for her own nest partitions.

Nests consisted of linear series of 2–12 brood cells. These cells varied from 5.5–12.0 mm in length or 60.0 to 322.0 mm<sup>3</sup> in volume depending on nest diameter. Lengths of brood cells averaged  $8.4 \pm 0.6$  mm (7.5–9.7;  $n = 21$ ) in nests with diameters of 3.2 mm and  $7.9 \pm 1.3$  mm (5.5–12.0,  $n = 52$ ) and  $7.9 \pm 1.4$  mm (6.5–12.0,  $n = 11$ ) for 4.8 and 6.4 mm diameter nests respectively. No consistent pattern was evident between brood cell length and its position within a nest. Too many bees escaped from nests without being sexed or were destroyed by parasites to allow accurate estimates of sex ratio or position of sexes within nests. Limited available data suggest that, as is common in sexually dimorphic, trap-nesting species with large females, females are produced primarily in the innermost cells. Only males were produced from the two 3.2 mm diameter nests. The provision mass was firm and uniformly moist (except for dry loose pollen along the walls), filling most of the cell. The outer face of the provision mass slanted towards the cell entrance, the upper part of the mass being the furthest from the entrance. Females inserted the posterior end of the egg in a moistened area on the upper third of the slanted face with the anterior portion of the egg remaining free but curving down over the provisions.

In addition to trap-nests, we observed females of *O. subfasciata* investigating





Figures 3–4. *O. subfasciata* cell and cocoon structure. Figure 3. Cross-section of anterior portion of cocoon with attached nest partition (12.2 $\times$ ). (a) partition of coarse sand and masticated plant material. (b) outer cocoon layer adhering to partition. (c) outer sheets of inner cocoon. (d) fibrous layer of nipple. (e) middle layer of inner cocoon. (f) innermost layer of inner cocoon. Figure 4. Cross-section of cocoon nipple (49 $\times$ ). (a) elaboration of middle layer of inner cocoon. (b) fibrous inner layer of nipple. (c) innermost layer of cocoon.

various small, empty snail shells at BFL where a single-celled bee nest was found in one of these shells by A. Hook (personal communication). Although the nest was destroyed when opening the shell, the plug was of the characteristic sand/plant mastic mix. This, along with its small size, suggests it was a *Disceratosmia* nest. *Osmia subfasciata* is the only *Diceratosmia* known to occur at BFL, and other small megachilines occurring there use different materials in their nest partitions. It thus seems likely that *O. subfasciata*, like *Osmia conjuncta* Cresson (Rau 1937), occasionally constructs nests in snail shells.

**Nest Construction.**—Nests were initiated by placing a thin layer of the sand/masticated plant material mix at the end of the burrow. Sand and plant material were collected on the same trip. At Sayersville, we repeatedly observed female *O. subfasciata* chewing leaf margins of *Helianthemum georgianum* Chapman (Cistaceae), forming a small ball which was held beneath the mandibles. The bee then moved to an area of loose sand and dropped the ball of chewed leaf material on the sand surface where she proceeded to chew and knead the ball as she rolled it over the soil surface incorporating soil/sand particles into the mass (Fig. 2). Individuals were observed to return to the same small one or two m<sup>2</sup> areas for five or more consecutive leaf-soil loads. Source of the plant material at other sites is unknown but presumably a variety of plant taxa is utilized. Upon returning to the nest, the female laid down a low rim of the soil/leaf masticate mix which served as the base of the partition separating the first two cells of the nest. Construction of such a rim, known as Fabre's threshold (Malyshev 1936) is widespread among megachiline bees (Frohlich 1983; JLN, personal observation). After provisioning and ovipositing in the first cell, the female closed the cell delimited by the initial rim and constructed another rim. This pattern continued until the final cell of the nest was completed.

Bee 87-7 required 11 trips and 97.7 minutes to finish a partition and construct a new rim. During this period she averaged  $6.3 \pm 1.73$  min (2.82–9.63;  $n = 11$ ) in the nest and  $2.58 \pm 2.34$  min (0.76–8.78;  $n = 11$ ) away from the nest. Female *O. subfasciata* apparently are able to construct and provision two cells per day.

The female observed in 1989 at BFL took six days to complete a 12 cell nest (89-7) and then six days for a nine cell nest (89-18).

*Provisioning Behavior.*—Because females in the small 3.2 and 4.8 mm diameter nests had to exit the nest to turn around to deposit pollen, time in the nest after pollen trips could be separated into nectar and pollen deposition components. Female 89-7 averaged  $0.76 \pm 0.19$  min ( $n = 11$ ) in the nest for nectar deposition and  $1.00 \pm 0.30$  ( $n = 11$ ) for pollen deposition. Female 87-7 was somewhat faster, averaging  $0.31 \pm 0.14$  ( $n = 9$ ) for nectar deposition and  $0.71 \pm 0.21$  for pollen deposition. The preceding times for pollen deposition exclude the long final period of a provisioning sequence which presumably represents final pollen mass preparation and oviposition. This final period was 5.35 min for bee 87-7, and 4.45 min for bee 89-7.

Interpretation of foraging patterns was complicated by the lack of consistency in the duration of pollen trips. A complete provisioning series for a male cell in nest 89-7, provisioned on 19 Apr 1989 required 192 minutes. This entailed 10 or possibly 13 pollen trips. The variable estimate stems from the fact that most pollen trips were relatively long, averaging  $16.05 \pm 2.78$  min (12.04–22.29;  $n = 9$ ) but there were also three short trips averaging only  $2.74 \pm 1.22$  min (2.02–4.15;  $n = 3$ ) when the bee returned with pollen. It is likely the short trips were not true pollen trips but we cannot be sure as we were not able to tell if the bee's scopa still contained pollen when she exited the nest. The female behaved as if she were depositing pollen prior to leaving for the apparent short pollen trips. Another cell provisioned on 1 Apr 1987 showed the same pattern. This cell required only 88 minutes and six long trips with a mean of  $15.07 \pm 4.66$  min (6.12–19.90) and four short ones with a mean of  $1.46 \pm 0.85$  min (0.89–2.71). A similar mix of long and short trips was observed in other partial provisioning series noted in 1987, 1989, and 1990. The short trips may have been nectar trips or perhaps represent a form of defensive behavior against nest parasites which oviposit in open cells.

*Development and Cocoon Structure.*—Larvae fed without moving from the initial position of egg insertion during the first three instars. The conspicuously setose fourth instar occurs six to seven days after hatching and then begins moving over the provision mass. Defecation is initiated one to two days after molting to the fourth instar. The pale, flattened fecal pellets are initially placed on the distal portions of the cell, particularly the distal walls and outer margins of the cap. Individual pellets free from the wall are curved, have tapered ends, and are 0.6–0.7 mm long. The curved, ventral surface of an individual pellet had a weakly defined, shallow, longitudinal groove. Pellets produced later become strongly flattened, even ribbon-like, as they are closely appressed to the cell wall or outer layer of the cocoon.

The cocoon consists of four layers in two distinct structures, an inner and outer cocoon (Fig. 3). The outer cocoon is single-layered and is initiated two to three days after molting to the final larval instar, well before the completion of feeding as two-thirds to three-fourths of the provision mass remains at that time. The initial portion of the outer cocoon layer consists of a tough translucent membrane placed over, and closely adhering to, the cell cap and anterior portions of the cell wall up to the edges of the remaining provisions. This portion of the cocoon is laid over the initial layer of fecal pellets. The outer cocoon is extended along the



cell walls, sometimes after the deposition of more fecal pellets, as the walls are exposed by continued feeding. Additional fecal pellets are deposited on the inner surface of this cocoon layer. The provisions are completely consumed roughly four to five days after the initiation of the outer cocoon. The outer cocoon is completed by covering the base of the cell after the completion of feeding.

The inner cocoon, initiated after the completion of the outer, required two or three days to construct and consisted of three layers. The outermost is formed by a series of thin, translucent sheets with a few embedded threads. These sheets are apparently laid down as overlapping series which are attached both to one another and to the outer cocoon. The innermost of these translucent sheets forms the foundation for the relatively thick (0.02 mm), tough, brown, opaque middle layer. Closely appressed to the inner surface of the middle layer is a thin, translucent inner layer.

The anterior end of the inner cocoon is elaborated into a nipple (Figs. 3, 4), a complex structure which apparently serves as an air exchange mechanism for the otherwise impervious cocoon. Seen from within, the innermost portion of the nipple appears as an opaque, smooth brown disk surrounded by a paler ring. In cross section, it can be seen that the disk is formed by a tightly packed region of the tough brown fibers which fill the mesal, hemispherical region of the nipple. The thick layer of tough threads is covered by, and grades into, the thickened continuation of the opaque middle layer of the cocoon. This thickened opaque layer is not continuous, having a central opening of approximately 0.3 mm. This central opening is filled with a continuation of the inner layer of coarse threads which in turn intergrades with dense translucent sheets covering the outer surface of the nipple.

*Osmia subfasciata* is univoltine in central Texas. After the completion of cocoon spinning, there is a relatively long larval diapause of approximately 90 to 110 days before pupation. Larvae completing cocoon construction by 6 May pupated by 5 Aug when kept in the lab at room temperature (23.3°–27.7° C). However larvae from a nest constructed at the same time but left in the field did not pupate until 30 Aug. Individuals overwinter as adults within their natal cocoons.

*Mating Behavior.*—Mating was rarely observed although males are commonly observed patrolling female pollen and nectar sources such as flowers of *Cercis*, *Nemophila* or *Berberis* during the initial portions of the flight season. Mating, including a period of post-copulatory mate guarding, was prolonged and was observed only at flowers. Males were never observed at nest sites or areas of female emergence when occupied trap nests were placed in the field. It is likely that female *O. subfasciata* mate only once, or at most a few times, during a brief receptive period.

*Predators and Parasites.*—Nest parasitism was not extensive with only two species of nest parasites reared. Bombyliid larvae were reared from two outer cells of BFL trap-nests. Pupal morphology indicated they were Anthracinae, presumably *Anthrax*, but neither individual was able to pierce the nest closure to exit and both failed to eclose. The other nest parasite was the small chrysid wasp, *Chrysura pacifica* (Say) which was reared from nests from Sayersville set out in 1986 and 1989. *Chrysura pacifica* has not been collected at BFL. Our observations of *C. pacifica* larval development agreed with earlier observations of *C. pacifica* attacking *Osmia pumila* Cresson (Krombein 1967: 446). The four-celled Sayers-



ville 89 nest included six *C. pacifica*: two cells with two *C. pacifica*, and two with one. The eggs have a thick, tough chorion and are deposited near the basal portion of the provisions. In a cell where larval development was followed completely, the *C. pacifica* egg hatched one day after the *O. subfasciata* egg (three to four days after *O. subfasciata* oviposition). The *C. pacifica* larva remained quiescent for three days before beginning to move forward over the provision mass, aided by an unusual bifurcate caudal segment. After two days of movement it reached and attached itself with its mandibles to the still sessile, third instar *O. subfasciata* larva. A second *C. pacifica* larva, previously hidden on the opposite side of the cell, attached itself to the *O. subfasciata* larva on the following day. The *O. subfasciata* larva molted to the fourth instar the following day (seven days after hatching) and both larvae were detached, with only one reattaching to the now setose, free moving *O. subfasciata* larva. The remaining first instar *C. pacifica* larva remained inactive but attached to the *O. subfasciata* larva for an additional 12 days, during which the *O. subfasciata* larva completed constructing its cocoon. It then began feeding on the *O. subfasciata* larva and its own growth became obvious. Feeding continued for five days, after which the *O. subfasciata* larva was badly shriveled. Unfortunately, the *C. pacifica* larva was killed by a laboratory infestation of *Chaetodactylus* mites which almost certainly came from infested nests of *Osmia ribifloris* Cockerell stored nearby. Mites developed from egg to adult on provisions and feces of *O. subfasciata* but no infestations were observed in field collected nests nor were mites present on adults.

Miltogrammine flies were common at the BFL nest site but apparently were associated with various sphecids and eumenid wasps using the domicile as none were observed at bee nest entrances. The surface of the pollen mass from one cell in nest 89-18 in which the egg failed to hatch was encrusted with the black fruiting bodies of *Ascosphaera*. The fungus was not noted in other cells. The only observation of predation was a female captured by the common red assassin bug, *Apiomerus spissipes* (Say), at flowers of *Verbena officinalis* Linnaeus ssp. *halei* (Small) Barber, at Pedernales Falls State Park, Blanco Co., Texas.

#### DISCUSSION

Our observations on nest structure and cocoon structure of *O. subfasciata* agree with those of the only previous study by Krombein (1967) in many features of general nest architecture but differ in a number of important aspects. Krombein reported that partitions in his nest from Scottsdale, Arizona, were constructed only of masticated leaf material rather than the sand/plant mix we found in Texas. Use of a combination of sand or soil and masticated leaf material for nest construction is common in the *Hoplitis-Anthocopa-Proteriades* complex, particularly in the subgenera *Pentteriades*, *Hoplitina*, *Xerosmia*, *Acrosmia*, *Atoposmia*, *Eremosmia* and *Hexosmia* (Parker 1975, 1978a, b). However, it apparently is uncommon in *Osmia* (sensu Sinha 1958). Published accounts indicate the vast majority of *Osmia* species use either soil or plant masticate in nest construction but not both (Iwata 1976, Rust 1974). Exceptions among American species include *Osmia* (*Cephalosmia*) *californica* Cresson, which constructs nest plugs and partition of a mix of mud and masticated plant material (Levin 1966, Rust 1974, Torchio 1989), and *Osmia* (*Trichinosmia*) *latisulcata* Michener, which uses a sand/plant masticate mix for cell partitions and plant masticate and pebbles for

nest plugs (Parker 1984). Both mud and plant masticate are used in constructing the urn-like cells of some members of subgenus *Acanthosmioides* (Rust et al. 1974). The use of a sand/plant masticate mix in nest construction appears to be unusual even within *Diceratosmia*. Nest construction materials in various species of *Diceratosmia* have been described as leaf paste (*O. conjuncta* [Rau 1937]), leaf pulp (*Osmia gallarum* Spinola [Iwata 1976]), and green putty (*Osmia versicolor* Latreille [Fabre 1915]). If *Diceratosmia* is actually the sister group of all other *Osmia* (sensu Sinha 1958), it is tempting to suggest that the sand/plant pulp mixture is the primitive nest construction material for this lineage, but the occurrence of mud, plant masticate, or various mixes as nest construction materials by taxa scattered throughout the genus renders this highly speculative.

Initiation of cocon spinning before the completion of feeding also appears to be unusual among megachilines. Although production of a few threads, which aid in holding the feces in place prior to cocoon completion, is common among megachilines (Stephen et al. 1969, Torchio 1989), production of a distinct sheet as produced by *O. subfasciata* is not. Unfortunately, there are relatively few studies of development which would allow one to ascertain accurately when cocoon-spinning is initiated. The only other megachiline we are aware of that regularly initiates cocoon construction well before completing feeding is *Hoplitis* (*Robertsonella*) *simplex* (Cresson) (JLN, personal observation).

There is considerable variation in cocoon structure within *Osmia*. The cocoon of *O. subfasciata* is a distinctive combination of elements found elsewhere in the genus. The tough, nipples, multilayered cocoons of *Osmia* s. str. (Rust 1974; JLN, personal observation) appear to be virtually identical to the inner cocoons of *O. subfasciata*. The presence of a well formed anterior layer of the outer cocoon is apparently more unusual in *Osmia* although a very similar structure is present in cocoons of *O. latisulcata* (Parker 1984). A well defined anterior portion of the outer cocoon is present in at least some species of *Hoplitis* and *Chelostoma* (Parker 1988; JLN, personal observation).

The extended prepupal diapause we observed in *O. subfasciata* also appears to be unusual among megachilines which overwinter as adults. A review of published reports suggests most *Osmia* larvae pupate within thirty days of cocoon completion. Significant exceptions are the two year individuals of parsivoltine species, which typically spend their first winter as prepupae (Torchio & Tepedino 1982) and larvae of *Osmia nigrifrons* Cresson that have prepupal diapause lasting 130–150 days (Rust et al. 1974). In addition, we have found that central Texas populations we studied of *Osmia ribifloris* have an extended prepupal diapause of 100–150 days (unpublished data) even though populations from northern Nevada have a brief prepupal diapause (Rust 1986). Although we are unaware of conclusive proof, it is generally believed that the prepupal stage of bees has lower metabolic requirements and is more resistant to environmental stress than the adult. Presumably this explains why the prepupal stage is the one most commonly used for overwintering or extended diapause.

Nonetheless, overwintering as an adult is common among cool-temperate bees which emerge in the early spring (Stephen et al. 1969). Overwintering as an adult presumably facilitates early emergence and avoidance of pupation under cold or otherwise unsuitable conditions. However, overwintering as an adult by vernal bees may regularly expose diapausing adults to potentially lethal temperatures



and/or moisture stress in areas of high summer temperatures. A recent study has shown that diapausing adult *Osmia cornifrons* Radoszkowski kept at 22° C had a survivorship rate (76%) nearly twice that of individuals maintained at 30° C (39.9%) (Maeta 1978). Excluding *Osmia*, most osmiine bees overwinter as prepupae so it is possible that the extended prepupal diapause we observed in *O. subfasciata* simply reflects retention of the plesiomorphic state. However, we believe that in *Osmia*, extended prepupal diapause is a derived condition facilitating tolerance of extended hot conditions, particularly those with high night temperatures such as are commonly encountered during central Texas summers. Average minimum monthly temperature exceeds 18° C from May through September in central Texas (Conway & Liston 1974). We expect extended prepupal diapause will be found in other *Osmia* spp. of central Texas as well as in other regions with high night temperatures. *Osmia subfasciata* larvae from Scottsdale, Arizona reared in a Washington, D.C. laboratory had a prepupal diapause of roughly 45 days (Krombein 1967). The pattern of overwintering as an adult during the winter before spring emergence, appears to be universal in *Osmia* and may be an important factor limiting the southern distribution of the genus. Two year old individuals in parsivoltine species of *Osmia* spend their first winter as prepupae, but their second as adults (Torchio & Tepedino, 1982). These cases represent an extreme form of extended prepupal diapause for some individuals. Extended prepupal diapause appears to be a mechanism which minimizes exposure of diapausing adults to the temperature and moisture stress in warm climes yet retains the flexibility for early spring emergence.

#### ACKNOWLEDGMENT

We thank Gregg Dieringer for assistance with SEM work, and the Texas Department of Parks and Wildlife for permission to collect at Pedernales State Park (permits 17-89 and 10-90). Gregg Dieringer also read the manuscript and made many helpful suggestions.

#### LITERATURE CITED

- Cockerell, T. D. A. 1911. Bees in the collection of the United States National Museum. 2. Proc. U.S. Nat. Mus., 40: 241-264.
- Conway, H. M. & L. L. Liston (eds.). 1974. The weather handbook (rev. ed). Conway Research Inc., Atlanta, Georgia.
- Correll, D. S. & M. C. Johnston. 1970. Manual of the vascular plants of Texas. Texas Research Foundation, Renner, Texas.
- Fabré, J. H. 1915. Bramble-bees and others. Dodd, Mead and Company, New York.
- Frohlich, D. R. 1983. On the nesting biology of *Osmia* (*Chenosmia*) *bruneri* (Hymenoptera: Megachilidae). J. Kansas. Entomol. Soc., 56: 123-130.
- Hurd, P. D., Jr. 1979. Superfamily Apoidea. pp. 1741-2209. In K. V. Krombein, P. D. Hurd, Jr., D. R. Smith & B. D. Burks (eds.). Catalog of Hymenoptera in America north of Mexico, Vol. 2, Apocrita. Smithsonian Institution Press, Washington, D.C.
- Hurd, P.D. Jr. & C. D. Michener. 1955. The megachiline bees of California (Hymenoptera: Megachilidae). Bull. Calif. Insect Survey, 3: 1-247.
- Iwata, K. 1976. Evolution of instinct: comparative ethology of Hymenoptera. Amerind Publishing Co. Pvt. Ltd., New Delhi.
- Johnston, M. C. 1988. The vascular plants of Texas. Privately published, Austin, Texas.
- Krombein, K. V. 1967. Trap-nesting wasps and bees: life histories, nests, and associates. Smithsonian Institution Press, Washington, D.C.

- Levin, M. D. 1966. Biological notes on *Osmia lignaria* and *Osmia californica* (Hymenoptera: Apoidea, Megachilidae). J. Kansas Entomol. Soc., 39: 524–535.
- Linsley, E. G. 1946. Insect pollinators of alfalfa in California. J. Econ. Entomol., 39: 18–29.
- Maeta, Y. 1978. Comparative studies on the biology of bees of the genus *Osmia* of Japan, with special reference to their managements for pollinations of crops (Hymenoptera: Megachilidae). Bull. Tohoku Nat. Agric. Exper. Sta., 57: 1–221.
- Malyshev, S. I. 1936. Nesting habits of bees. Eos 11: 201–309.
- Michener, C. D. 1979. Biogeography of the bees. Ann. Missouri Bot. Gard., 66: 277–347.
- Mitchell, T. B. 1962. Bees of the eastern United States, Volume II. North Carolina State University Agric. Sta. Tech. Bull., 152: 1–557.
- Parker, F. D. 1975. Nest descriptions and associates of three American bees of the genus “*Anthocopa*” Lepeletier. (Hymenoptera: Megachilidae). Pan-Pacif. Entomol., 51: 113–122.
- Parker, F. D. 1978a. Biology of the bee genus *Proteriades* Titus (Hymenoptera: Megachilidae). J. Kansas Entomol. Soc., 51: 145–173.
- Parker, F. D. 1978b. Nests of *Anthocopa enceliae* (Cockerell) and *A. elongata* (Hymenoptera: Megachilidae). Pan-Pacif. Entomol., 53: 47–52.
- Parker, F. D. 1984. The nesting biology of *Osmia* (*Trichinosmia*) *latisulcata* Michener. J. Kansas Entomol. Soc., 57: 430–436.
- Parker, F. D. 1988. Nesting biology of two North American species of *Chelostoma* (Hymenoptera: Megachilidae). Pan-Pacif. Entomol., 64: 1–8.
- Rau, P. 1937. Life history of *Osmia lignaria* and *Osmia cordata* with notes on *Osmia conjuncta*. Ann. Entomol. Soc. Am., 30: 324–343.
- Rust, R. W. 1974. The systematics and biology of the genus *Osmia*, subgenera *Osmia*, *Chalcosmia*, and *Cephalosmia* (Hymenoptera: Megachilidae). Wasmann J. Biol., 32: 1–93.
- Rust, R. W. 1986. Biology of *Osmia* (*Osmia*) *ribifloris* Cockerell (Hymenoptera: Megachilidae). J. Kansas Entomol. Soc., 59: 89–94.
- Rust, R. W., R. W. Thorp & P. F. Torchio. 1974. The ecology of *Osmia nigrifrons* with a comparison of other *Acanthosmioides*. J. Nat. Hist., 8: 29–47.
- Sinha, R. N. 1958. A subgeneric revision of the genus *Osmia* in the western hemisphere (Hymenoptera: Megachilidae). Univ. Kansas Science Bull., 39: 211–261.
- Stephen, W. P., G. E. Bohart & P. F. Torchio. 1969. The biology and external morphology of bees. Agric. Exp. Station, Oregon State University. Corvallis, Oregon.
- Torchio, P. F. 1989. In-nest biologies and development of immature stages of three *Osmia* species (Hymenoptera: Megachilidae). Ann. Entomol. Soc. Am., 82: 599–615.
- Torchio, P. F. & V. J. Tepedino. 1982. Parsivoltinism in three species of *Osmia* bees. Pan-Pac. Entomol., 51: 113–122.

*Received 18 January 1991; accepted 1 June 1990.*